Distribution of Western Spruce Budworm Egg Masses on White Fir and Douglas-fir

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Abstract

Differences among trees and crown levels usually contributed significant variation to egg mass (EM) counts, while differences among aspects and between branches within the same crown level did not. When EM's per branch differed significantly among crown levels, branch size accounted for most of the difference. EM's per square meter of foliage of Douglas-fir were not generally significantly different among crown levels. EM's per square meter of foliage of white fir were significantly greater in the upper crowns than in the middle and lower crowns more than 50% of the time. The importance of each source of variation is discussed in relation to current EM-sampling techniques.

[1]*Headquarters is in Fort Collins, in cooperation with Colorado State University.*

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Management Implications

Sampling procedures currently used to predict defoliation from egg mass (EM) counts could be changed to increase precision. Differences among trees contribute a significant amount of variation to EM counts, so the number of sample trees should be as large as possible (see Discussion). Differences among crown levels also contribute significant variation, but the lower and middle levels are usually not different, so EM surveys can sample from either level. Differences among branches and aspects within the same crown level of a tree do not contribute significant variation, so only one branch need be removed from any side in the midcrown. If current sampling procedures are modified to use only one midcrown branch from six or more trees per cluster, the time spent sampling each tree will decrease, but sampling time for the cluster will increase. The cost of sampling each cluster may remain about the same or increase significantly, depending on how many additional trees are sampled, but the precision of the estimated EM density should also increase. Defoliation predictions for a mixed stand of Douglas-fir and white fir will overestimate the defoliation on white fir if defoliation is proportional to EM density, because densities are generally greater on Douglas-fir.

Introduction

Sampling methods for 3 predicting defoliation by the western spruce budworm, *Choristoneura occidentalis* Freeman, exclusively use branch samples from 11 Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. This practice is quite valuable when comparing budworm densities on the same host in widely separated geographical areas, for example, Montana versus New Mexico. It has also allowed the establishment of standardized sampling so that Forest Service EM survey procedures are similar in the West.

Sampling one host is inadequate, however, when two or more hosts are mixed and a defoliation estimate for the other host is needed. Because major emphasis has been placed on Douglas-fir, little information has been developed on the distribution of budworms on other hosts. Thus, defoliation prediction techniques for Douglas-fir are questionable when used on other hosts, such as white fir, *Abies concolor* (Gord. and Glend.) 12 Lindl.

This study was initially conducted to determine the EM distributions on white fir. Later, the study was expanded to examine EM distribution in mixed stands of white fir and Douglas-fir. More specifically, it sought to determine the distribution of EM's with respect to host species, trees, crown levels, and aspects.

Methods

EM-bearing branches were collected from three crown levels on host species from locations specified in table 1. The locations were selected because they had easily accessible trees with abundant budworm populations and because they were in different geographic areas. Collection areas were about 1 ha in size, except for the Los Alamos location, which was several hectares.

Whole branches were pruned from trees in 1977 and 1978. However, whole branches from the middle and lower crowns of white fir and, occasionally, Douglas-fir exhibited dichotomy and were really composed of two or more branchlets. These branchlets often lacked live needles at their connecting base, so they were considered separate branches. Furthermore, because whole branch examination was impractical for the data it yielded, branchlets were removed from the middle and lower crowns in 1979 and 1980. Whole branches were still removed from the upper crowns in these years. The branches were put in sacks and transported to cold storage units in Fort Collins.

In 1977, each branch was cut into 15-cm-long segments beginning at the tip and working toward the base of the branch along the primary stem. New EM's per segment were recorded and numbers per branch were compared using analysis of variance, testing for significant variation among trees, crown levels, aspects, and branches, $P = 0.05$. Numbers per respective 15-cm segment were used in two ways: (1) to compute mean percent of EM's for 1- to 15-cm, 15- to 30-cm, 30- to 45-cm, and >45-cm branch segments and (2) to compute the mean number in cumulative (0- to 15-cm, 0- to 30-cm, 0- to 45-cm) branch segments.

In 1978, each branch was measured metrically for length and width and assigned a form, either triangular or rectangular, whichever best approximated its shape, in order to later determine branch area. The branches were then examined for EM's in two ways: (1) half of the branches (one branch from each aspect/crown-level combination) were inspected in 14-cm-long segments be-

Table 1.—Sampling information regarding collection of EM-bearing branches

Year	Collection location near	Host species	Number of trees	Number crown levels	Aspects	Branches per crown level	Collection dates
1977	La Veta and Rye, Colo.	White fir	20	3	2	4 (2N, 2S)	September 13, 1977
1978	Los Alamos, N. Mex.	White fir	25	3	2	4 (2N, 2S)	July 24 - August 3, 1978
	Taos, N. Mex.	White fir	25	3	2	4 (2N, 2S)	July 24 - August 3, 1798
	Vallecito Reservoir, Colorado	White fir	25	3	2	4 (2N, 2S)	July 24 - August 3, 1978
	La Veta Pass, Colorado	White fir	25	3	2	4 (2N, 2S)	July 24 - Augsut 3, 1978
1979	Los Alamos, N. Mex.	White fir	25	3	—[1]	1	July 31 - August 2, 1979
		Douglas-fir	24	3	—	1	July 31 - August 2, 1979
	Vallecito Reservoir, Colorado	White fir	17	3	—	1	September 26-27, 1979
		Douglas-fir	17	3	—	1	September 26-27, 1979
1980	Los Alamos, N. Mex.	White fir	10	3	—	1	August 5-7, 1980
		Douglas-fir	10	3	—	1	August 5-7, 1980
	Taos, N. Mex.	White fir	10	1	—	1	August 5-7, 1980
		Douglas-fir	10	1	—	1	August 5-7, 1980
	Vallecito Reservoir, Colorado	White fir	10	3	—	1	August 13-14, 1980
		Douglas-fir	10	3	—	1	August 13-14, 1980
	La Veta Pass, Colorado	White fir	10	3	—	1	August 21, 1980
		Douglas-fir	10	3	—	1	August 21, 1980

[1]*After 1978, aspects were disregarded and branches taken from any side of the tree.*

ginning at the tip or where live foliage began and working toward the base of the branch and (2) the other half of the branches were examined in 14-cm-wide concentric bands which began on the outer edges of the foliage and progressed inwardly. EM's were removed, classified as new or old, and the number of new EM's recorded with the branch measurements. After examination, the foliage was stripped from the stems and sacked in paper bags. The foliage was later dried for 24 hours at 100° C to obtain its oven-dry weight. Branch exámination was unexpectedly slow because foliage removal was slower than expected. Some branches then deteriorated in cold storage when, because of the delay, mold frequently developed or the needles dehydrated, dropping from the stems. Deterioration prevented examination of all branches from each location. The data were thus only partially complete. Where possible, EM's per branch, per square meter, and per 100 g of foliage were analyzed for differences among trees and crown levels but not aspects or branches.

In 1979, and 1978 study was repeated, except that only one branch was removed per crown level, Douglas-fir branches were collected simultaneously, and the branches were only examined in 14-cm units beginning at the tip and working toward the base.

The EM information was assembled into three categories: (1) new EM's per branch, (2) new EM's per square meter of foliage, and (3) new EM's per 100 g of foliage. Each category was analyzed in a three-way analysis of variance testing for significant variation associated with host species, trees, and crown levels, $P = 0.05$. If significant interaction existed between hosts and crown levels, a one-way analysis of variance was executed for each host to affirm or deny significant differences in crown levels.

The 1980 branches were collected and examined as in 1979, except that the foliage was not dried and weighed. The number of new EM's per branch and per square meter of foliage were analyzed using analysis of variance testing for significant differences among host species, trees, and crown levels, $P = 0.05$. When crown-level variation appeared inconsistent between hosts, a separate one-way analysis was used to test for significant differences among crown levels for each host. Using the number of EM's in each 14-cm segment, the percentage of EM's in segment 1, segments 1 and 2, segments 1, 2, and 3, and so forth, were determined.

Results

Sources of Variation in Egg Mass Counts

EM's per branch varied significantly among trees and crown levels in 1977 (table 2). Aspects, branches, and aspect/crown-level interaction contributed insignificant variation. Crown levels contributed the most variation, at least three times the amount contributed by trees.

Data from 1978 were insufficient to determine the significance of each source of variation. Nevertheless, by inspection, trees and crown levels appeared important, while aspects appeared unimportant, as demonstrated in the 1977 data.

In 1979, the amount of variation contributed by each factor varied among locations and among the basis for comparison (branch, branch area, or branch weight).

Host species contributed significant and greater amounts of variation in all three analyses (EM's per branch, per square meter, and per 100 g) of the Vallecito Reservoir data, while host species at Los Alamos contributed less variation than crown levels in all three analyses and significantly in only the analysis of EM's per 100 g. Crown levels contributed significant variation in the EM's per square meter and per 100 g analyses for both locations but insignificant variation in the analyses of EM's per branch of the Vallecito Reservoir data (table 2). Host species and crown level interacted significantly in the analyses of EM's per branch and EM's per square meter for the Vallecito Reservoir data and was nearly significant in the analysis of EM's per 100 g of the Los Alamos data. The interaction was usually significant when the variation associated with hosts was different. Trees contributed significant variation in the analysis of EM's per branch for both locations and for the analyses of EM's per square meter and EM's per 100 g of the Los Alamos data.

In 1980, host species contributed significant variation in EM counts at Los Alamos and La Veta Pass for both types of analyses (table 2), Douglas-fir having significantly higher counts than white fir. Variation contributed by crown levels was only significant at Vallecito Reservoir and La Veta Pass for the analysis of EM's per branch, although crown-level differences within each species at La Veta Pass were not significantly different. Interactions between host species and crown levels were never significant. Trees contributed significant variation in the analyses of EM's per branch for three of four locations but contributed significant variation for only Vallecito Reservoir in the analyses of EM's per square meter.

Mean Number of Egg Masses per Branch, per Square Meter of Foliage, and per 100 g of Foliage

In 1977, EM's per midcrown branch were significantly greater than on lower crown branches (table 3). EM's per branch, per square meter, and per 100 g of foliage were highest in the upper crown in 1978 (table 3).

EM counts for Douglas-fir and white fir in 1979 exhibited similar relationships for the two locations (table 3). On a per branch basis, EM's on Douglas-fir were greatest in the middle crown (40 at Los Alamos and 21 at Vallecito Reservoir) and significantly lower in the upper crown (22 and 11 for the two respective locations), while counts on white fir were not different among crown levels. EM's per square meter of foliage on Douglas-fir were not different among crown levels while upper crown means of 96 and 36 on white fir were significantly greater than respective middle (51, 21) and lower (41, 12) crown means. EM's per 100 g of foliage followed the same relationships for each host as EM's per square meter—no difference among crown levels for Douglas-fir and greater numbers in the upper crown for white fir. EM densities on Douglas-fir were the same or higher than on white fir (table 3). Densities in the upper crown were similar for the two species while Douglas-fir had greater densities in the lower and middle crowns.

In 1980, mean numbers of EM's per branch were insignificantly highest in midcrown on both hosts (table 3). Mean numbers per square meter were highest in the upper crown of both hosts at Los Alamos but varied between upper and middle crown by host at Vallecito Reservoir and La Veta Pass. Densities were generally greater on Douglas-fir than on white fir.

Table 2.—Sources of variation in EM counts[1]

Variable Source of variation	1977 San Isabel National Forest, Colorado	1979 Vallecito Reservoir, Colorado	1979 Los Alamos, N. Mex.	1980 Los Alamos, N. Mex.	1980 Taos, N. Mex.	1980 Vallecito Reservoir, Colorado	1980 La Veta Pass, Colorado
EM's per branch							
Host species (HS)	—	S	NS	S	NS	NS	S
Trees	S	S	S	S	NS	S	S
Crown levels (CL)	S	NS	S	NS	—	S	S
Aspects (A)	NS	—	—	—	—	—	—
Branches	NS	—	—	—	—	—	—
CL x A	NS	—	—	—	—	—	—
HS x CL	—	S	S	NS	—	S	NS
EM's per square meter of foliage							
Host species (HS)	No data	S	NS	S	NS	NS	S
Trees		NS	S	NS	NS	S	NS
Crown levels (CL)		S	S	NS	—	NS	NS
HS x CL		S	NS	NS	—	NS	NS
EM's per 100 g of foliage							
Host species (HS)	No data	S	S	No data	No data	No data	No data
Trees		NS	S				
Crown levels (CL)		S	S				
HS x CL		NS	S				

[1]*S = significant at the 0.05 level*
NS = nonsignificant
— = not able to determine because of sampling design

Table 3.—Mean number of new EM's per branc
oven-dry weight of foliage for Douglas-fir an

Variable Crown level	1977 San Isabel National Forest, Colorado	1978 Los Alamos, N. Mex.	1979 Los Alamos, N. Mex.		1979 Vallecito Reservoir, Colorado		1 Los N.
	White fir	White fir	Douglas-fir	White fir	Douglas-fir	White fir	Douglas-fir
EM's per branch							
Upper	5ab ± 7	9a ± 9	22a ± 11	34a ± 22	11a ± 10	14a ± 12	16a ± 11
Middle	8a ± 8	5ab ± 7	40b ± 27	35a ± 23	21b ± 12	10a ± 6	27a ± 18
Lower	3b ± 3	3b ± 4	32ab ± 24	26a ± 26	17ab ± 14	7a ± 6	21a ± 11
EM's per square meter of foliage							
Upper	No data	22a ± 19	84a ± 50	96a ± 60	38a ± 22	36a ± 24	49a ± 33
Middle		11b ± 13	74a ± 56	51b ± 32	55a ± 31	21b ± 11	40a ± 24
Lower		11b ± 13	59a ± 51	41b ± 69	35a ± 26	12b ± 9	38a ± 25
EM's per 100 g of foliage							
Upper	No data	5a ± 4	15a ± 7	17a ± 10	9a ± 4	7a ± 4	No data
Middle		3b ± 3	14a ± 6	10b ± 5	9a ± 4	6ab ± 3	
Lower		3b ± 3	12a ± 7	8b ± 5	7a ± 4	4b ± 2	

[1]*Means within a set of crown levels for a particular host which are followed by the same letter are not significantly different according to Tukey's multiple comparison procedure, P = 0.05.*

Within-branch Distribution of Egg Masses

The percent of new EM's per 15-cm branch segments of white fir in 1977 followed the same pattern in the crown levels of the north and south sides except for the lower south level (table 4). Percentages of EM's in the first 30 cm ranged from 9% to 25% of the total EM's per branch.

Percent of new EM's on cumulative 14-cm units was generally slightly higher for respective segments from a middle crown branch of white fir than for Douglas-fir in 1979 (table 5). White fir had 9% of the total EM's in the first 28 cm, while Douglas-fir had 6% (table 5). For the first 70 cm (5 14-cm units), white fir had 33-41% of the total EM's, Douglas-fir had 28-29%.

In 1980, the percentage of new EM's in the 14- and 28-cm segments was slightly greater than for each host in 1979. However, the 1980 percentages for the 70-cm length were 5-20% greater than for the respective hosts in 1979 (table 5).

Table 4.—Distribution of new EM's on cumulative 15-cm branch segments of white fir, 1977

Aspect Crown level	Cumulative branch segments			
	0-15 cm	0-30 cm	0-45 cm	>45 cm
	cumulative percent			
North				
Upper	4	13	37	100
Middle	2	15	40	100
Lower	2	16	38	100
South				
Upper	3	9	28	100
Middle	6	14	25	100
Lower	15	25	46	100

Discussion

Egg Mass Variation—Sampling Relationships

The significant variation contributed by trees and crown levels and the insignificant variation contributed by branches and aspects agree with the results of Morris (1955) for balsam fir, *Abies balsamea* (L.) Mill. and of Harris and Edwards (1960) for subalpine fir, *Abies lasiocarpa* (Hook.) Nutt. Variation among crown levels in this study was generally larger than among trees, just the opposite of Morris's results. Carolin and Coulter (1972) also found occasional significant differences in crown levels of Douglas-fir, especially when EM's were expressed on a per branch basis rather than per 1,000 square inches. In later studies of grand fir, *Abies grandis* (Dougl. ex D. Don) Lindl., Carolin and Coulter (1975) found significant differences in EM's per 1,000 square inches among crown levels. The insignificant variation associated with branches (within tree) differs from the results of Carolin and Coulter (1959),[2] who found significant within-tree variation in the same crown level.

Each significant source of variation relates to the current EM survey procedure. In recent years, the EM counts from annual surveys have explained between 22% and 65% of the subsequent defoliation in three Forest Service Regions in the West (USDA Forest Service 1978). Many factors contribute to these low correlations, some of which can be attributed to the significant sources of variation.

[2]*Carolin, V. M., and W. K. Coulter (1959). Research findings relative to the biological evaluation of spruce budworm infestations in Oregon. Preliminary draft to aid in discussion at Western Forest Insect Work Conference, Ogden, Utah, March 1960. Draft on file at Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo.*

Table 3.—Mean number of new EM's per branch, per square meter of foliage, and per 100 g of oven-dry weight of foliage for Douglas-fir and white fir, 1977–1980

Variable Crown level	1977 San Isabel National Forest, Colorado	1978 Los Alamos, N. Mex.	1979 Los Alamos, N. Mex.		1979 Vallecito Reservoir, Colorado		1980 Los Alamos, N. Mex.		1980 Taos, N. Mex.		1980 Vallecito Reservoir, Colorado		1980 La Veta Pass, Colorado	
	White fir	White fir	Douglas-fir	White fir	Douglas-fir	White fir	Douglas-fir	White fir	Douglas-fir	White fir	Douglas-fir	White fir	Douglas-fir	White fir
	$\bar{x}$ ± S.D.[1]													
EM's per branch														
Upper	5ab ± 7	9a ± 9	22a ± 11	34a ± 22	11a ± 10	14a ± 12	16a ± 11	9a ± 7			18a ± 12	11a ± 6	5a ± 4	2a ± 2
Middle	8a ± 8	5ab ± 7	40b ± 27	35a ± 23	21b ± 12	10a ± 6	27a ± 18	8a ± 8	34 ± 15	24 ± 20	20a ± 14	28b ± 16	11a ± 8	5a ± 4
Lower	3b ± 3	3b ± 4	32ab ± 24	26a ± 26	17ab ± 14	7a ± 6	21a ± 11	4a ± 5			19a ± 18	13a ± 7	11a ± 9	4a ± 3
EM's per square meter of foliage														
Upper	No data	22a ± 19	84a ± 50	96a ± 60	38a ± 22	36a ± 24	49a ± 33	26a ± 21			84a ± 79	52a ± 24	10a ± 8	4a ± 4
Middle		11b ± 13	74a ± 56	51b ± 32	55a ± 31	21b ± 11	40a ± 24	14ab ± 8	79 ± 27	58 ± 39	53a ± 32	65a ± 30	12a ± 8	7a ± 3
Lower		11b ± 13	59a ± 51	41b ± 69	35a ± 26	12b ± 9	38a ± 25	8b ± 10			55b ± 50	52a ± 29	13a ± 7	7a ± 10
EM's per 100 g of foliage														
Upper	No data	5a ± 4	15a ± 7	17a ± 10	9a ± 4	7a ± 4	No data	No data	No data	No data	No data	No data	No data	No data
Middle		3b ± 3	14a ± 6	10b ± 5	9a ± 4	6ab ± 3								
Lower		3b ± 3	12a ± 7	8b ± 5	7a ± 4	4b ± 2								

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Each significant source of variation relates to the current EM survey procedure. In recent years, the EM counts from annual surveys have explained between 22% and 65% of the subsequent defoliation in three Forest Service Regions in the West (USDA Forest Service 1978). Many factors contribute to these low correlations, some of which can be attributed to the significant sources of variation.

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The current EM survey procedure is to remove two midcrown branches from each of three trees in a cluster, with the clusters scattered but established in specific locations throughout the entomological unit. This procedure supplanted that of McKnight et al. (1970) on National Forests because of a desire to obtain annual information on population trends in addition to defoliation predictions. The 3-tree-cluster procedure evolved from two sources: (1) the outstanding work of Morris (1955), who used cluster sampling for population dynamics work in 25-acre stands in New Brunswick and (2) an unpublished study in the Pacific Northwest Region, USDA Forest Service, which showed through multistage analyses of larval counts in opening buds, the 3-tree, 2-branch sample to be the most precise for the allocation of the resources (Twardus 1980 personal communication). Although three trees, instead of the one tree used by McKnight et al. (1970), should improve the precision, the poor to fair correlations of defoliation with EM counts suggests additional improvements need to be made if the procedure is used in the future.

Some inadequate correlations may result from too few clusters being sampled in the entomological unit. McKnight et al. (1970) recommended at least 25 1-tree plots be sampled. Sampling 9 3-tree plots would provide the branch equivalent to 25 1-tree plots, but the lesser number of plots may not encompass the variation within the unit. If the three trees in a cluster are fairly homogeneous, then the three trees essentially represent the equivalent of one tree, and 25 or more

Table 5.—Distribution of new EM's on cumulative 14-cm segments of midcrown branches of Douglas-fir and white fir

Location Date, Host	Distance from tip (cm)					
	≤14	≤28	≤42	≤56	≤70	≤84
	cumulative percent					
Los Alamos, N. Mex.						
1979, Douglas-fir	2	6	13	20	28	39
White fir	2	9	19	28	41	52
1980, Douglas-fir	2	9	15	25	37	49
White fir	3	11	31	39	54	61
Taos, N. Mex.						
1980, Douglas-fir	1	11	25	36	46	47
White fir	2	9	20	37	45	62
Vallecito Reservoir, Colorado						
1979, Douglas-fir	2	5	12	19	29	36
White fir	2	7	14	25	33	46
1980, Douglas-fir	5	10	15	20	34	45
White fir	3	11	24	35	53	66

clusters may have to be taken to obtain the equivalent of the 25 1-tree plots of McKnight et al. (1970).

Another factor contributing to low correlations may be the number of trees in the cluster. While the data from this study do not allow evaluation of among-tree variation to cluster sampling, the fact that trees contribute significant variation suggests that the most appropriate number of trees per cluster and the number of clusters per unit need to be determined.

Sampling two branches per tree is unwarranted because the results of Morris (1955), Harris and Edwards (1960), and this study, all indicate branches from the same crown level do not contribute significant variation. Morris (1955) mentions two other pertinent considerations: (1) "The use of a smaller sample unit such as one branch per tree is to be recommended for less exacting purposes such as insect survey" and (2) "There is little advantage in drawing more than one sample unit per tree, unless the time acquired to move from tree to tree is very high in relation to the time required to draw and examine one sample unit." Stands in southern Colorado/northern New Mexico are more open-grown with greater distances between trees than in balsam fir stands in New Brunswick, so maneuverability is enhanced and costs for sampling one branch from six trees would not be substantially different than sampling two branches from three trees. Thus, the precision of the estimate could be increased by taking one branch from each of a greater number of trees.

Crown-level differences will not affect the accuracy of the defoliation estimate if samples are drawn from the lower and middle crowns. Because middle and lower crown EM densities were not generally significantly different (table 3), either level can be sampled. Sparsely foliated branches from the extreme lower crown should be avoided, but, otherwise, any branch from the lower and middle crowns could be selected.

Another factor affecting the correlation between EM counts and defoliation may be the within-branch distribution of EM's. Carolin and Coulter (1959) found 34-59% of the EM's on 15-inch (38-cm) samples from five locations over a 3-year period. The mean percentage of new EM's per 70-cm sample from Douglas-fir ranged from 28% to 46% (table 5), and variation around the means was large. If a mean value for the 70-cm sample remained within this range throughout the life of an infestation, then better correlation between EM counts and defoliation might be expected. However, changes in this percentage as defoliation varies could partially explain the lack of good correlation between EM counts and defoliation (see Grimble and Young 1977).

The importance of stand density, stand composition, and site on variation in EM densities remains relatively undetermined. Williams et al. (1971) determined larval densities to be related to basal area and tree species, so these factors may contribute significantly to EM densities. If stand characteristsics are a factor, different numbers of trees may have to be sampled in the various stands to acquire the same relative precision. In current EM surveys, a mixture of 3-tree cluster plots from dense and open stands may be creating some imprecision and causing poorer correlation between EM densities and subsequent defoliation.

The margin of error for estimates of EM density has been of little concern in past surveys. Based on data from this study, densities with an error margin of 10% of the mean would require samples from more than 75 trees per area. This intensity may be prohibitive for budworm surveys so a less precise estimate must be accepted. Assuming each tree from this study represents a homogeneous cluster, then estimates of EM density with an error margin of 20% with a 95% probability could be achieved by sampling 20 to 30 clusters in most cases. Future work should investigate which combination of clusters, trees per cluster, and branches per tree yield the most precise and cost-effective estimate.

Host Species and Defoliation Prediction

The relationship between EM densities on Douglas-fir and other hosts is important because defoliation prediction techniques are currently available for only Douglas-fir. If defoliation on other hosts would be the same or less than on Douglas-fir, then the current prediction plan could be used in a mixed stand of hosts. Optimism must be guarded in this case because Carolin and Coulter (1975) found greater bud-killing on grand fir than on Douglas-fir even though EM denisities were similar for the two hosts. In this study, if defoliation was proportional to EM per square meter for Douglas-fir and white fir, then defoliation should be similar in the upper crowns of both species in 1980 and greater on Douglas-fir in 1981. Defoliation in the lower and middle crowns of Douglas-fir should be greater in both years than on white fir. If defoliation for the stand is based on Douglas-fir defoliation, then it would be overestimated because white fir would suffer less damage below the upper crown. In contrast, larval densities in 1979 were higher on white fir than on Douglas-fir, so that if the EM relationship between white fir and Douglas-fir was similar to that of 1979 and 1980, the greater larval survival on white fir may compensate for the lesser EM densities and result in an underestimate of white fir defoliation.

Factors Causing Significant Differences in Egg Mass Densities

Significant differences in EM's per branch result from significantly different branch sizes. Schmid and Morton (1981) found upper crown branches of Douglas-fir and white fir had significantly less area than middle crown branches. Even though eggs may be deposited in greater densities on upper crown branches (see square meter data, table 3), the smaller size of these branches causes the total numbers of EM's to be considerably less than on middle crown branches.

The generally insignificant differences in EM densities per square meter or per 100 g of foliage among

crown levels of Douglas-fir is not readily explainable. Significant interaction between crown levels and trees may have masked crown-level differences. Female moths may oviposit equally on all suitable branches in the crown levels of Douglas-fir, although this seems unlikely because they appear to oviposit a greater density of EM's in the upper crowns of white fir.

New EM's in different crown levels of white fir were significantly different per branch at only Vallecito Reservoir in 1980. They were significantly different per square meter at Los Alamos in 1979 and 1980 and at Vallecito Reservoir in 1979 (table 3) where the upper crown level density was significantly greater than the lower crown level and midcrown densities were usually intermediate to the upper and lower crown values. Female moths apparently oviposit a higher density of EM's in the upper crowns of white fir.

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Host species, trees, and crown levels usually contributed significant variation to egg mass counts, while aspects and branches within a crown level within a tree did not. This information is discussed in relation to sampling.

Keywords: Western spruce budworm, *Choristoneura occidentalis*

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